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INHERITANCE OF FLOWER SIZE IN CROSSES BETWEEN
SPECIES OF *NICOTIANA*¹

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(WITH PLATES VI-X)

Since the independent investigations of NILSSON-EHLE and of the writer demonstrated the feasibility of using the Mendelian notation to describe the inheritance of size characters that blend in the first hybrid generation, a number of botanical papers have appeared that supported this interpretation. These papers have considered the behavior in crosses of such characters as height of plant, size of leaf, number of leaves, time of flowering, and size of fruit. If the number of leaves in certain plants is excluded, this type of character is one particularly affected during development by external conditions. Since fluctuations produced in this manner are not transmitted, if the conclusions drawn from the sum total of our limited experimental cultures are to be given weight, the validity of the evidence in these investigations is not disturbed. At the same time, one must admit that these fluctuations obscure an analysis of the crude data. For example, plant *B* may be six inches higher than plant *A* when both are grown in the same environment, owing to a different heritage, but plant *A* may grow considerably higher than plant *B* if the environment of *A* is the best possible for maximum growth and the environment of *B* is poor.

In this paper, therefore, I propose to consider the inheritance of

¹ Contribution from the Laboratory of Genetics, Bussey Institution of Harvard University.

a character-complex which I believe to be the least affected by external conditions of any character that shows marked varietal differences. This character-complex is corolla size. The fact that corolla size is so comparatively constant under all conditions attending development has such a definite bearing on some broad questions of organography that it merits separate discussion. On this account, the liberty of asserting the truth of the statement with only the following data in its support is requested.

During the past four years, I have grown about 20 species of *Nicotiana* in considerable numbers. They have been grown under very diverse conditions. Some have been starved in four-inch pots, others have had the best of greenhouse treatment; some have had poor field conditions, others have had all field conditions practically at their best. The height of the plants, the size of the leaves, and similar size complexes have varied enormously, but the size of the corollas has scarcely varied at all. For example, plants of *Nicotiana silvestris* Speg. and Comes grown to maturity in four-inch pots produced no leaves longer than 7 in. On the other hand, sister plants of the same pure line produced leaves 30 in. long in the field. Both series, however, produced flowers with the same length and spread of corolla. Furthermore, cuttings from 20 of the field plants reported in this study were rooted and grown in small pots in the greenhouse. Their blossoms were the same size as those of the field grown plants from which they came.

The material used in this particular experiment consisted of pure lines of two *Nicotiana* types that are generally treated as distinct species (pl. VI). The male parent was *Nicotiana alata grandiflora* Comes, it being the plant called *Nicotiana affinis* by horticulturists. Three lots of it were under observation; one was obtained from Italy and the other two from the United States, but the original sources of the strains are unknown. These three lots were alike, and in successive generations were constant in their characters. They accorded perfectly with Comes' description and were remarkably narrow in their variability. The female parent I have called *Nicotiana forgetiana*, Hort. Sand., and thereby hangs a tale. I found in the Gray Herbarium of Harvard University a sheet from near Los Angeles, California, marked *Nicotiana clevelandii* Gray.

This designation was manifestly incorrect, as the plant was exactly like SANDER'S figure of *N. forgetiana* in the *Botanical Magazine* (No. 8006). As it had been collected only a few years, I took seed from one of the capsules and planted it. It grew and again produced plants like *N. forgetiana*. Miss DAY, the librarian of the Gray Herbarium, then looked up the correspondence regarding the specimen and found that it was evidently a garden specimen grown by a Californian botanist, since deceased, from seed furnished by Sander & Sons and called *N. Sandarae*. The plants have not the mixed colors and the variability of the specimens now sold as *Sandarae* hybrids, but are constant in their characters and are identical with *Nicotiana forgetiana*. I have come to the conclusion, therefore, that I have obtained (as LOCK² probably did) seeds of the real *N. forgetiana* that had been mixed with the *Sandarae*³ hybrids by Sander & Sons.

In view of the fact that *N. alata grandiflora* and *N. forgetiana* do not differ essentially in their foliage and habit of growth, but only in flower size and color—the one being white, the other red—perhaps one should not call them two species. I hold no brief either way. I simply accept the taxonomic ruling. At least, there existed here two strains very different from each other and very constant in their characters. Both were self-fertile, and in fact were usually self-pollinated naturally. They were crossed. There was no trouble about this, as every cross attempted was successful, and the capsules were filled with seeds.

This, then, seemed to be an excellent opportunity for studying size inheritance: two strains, uniform in pure lines, one with a corolla three times the length of the other, could be crossed easily. All was not plain sailing, however, for the plants of the *F*₁ generation (pl. VII) were absolutely self-sterile. This fact would have cut off the experiment in the flower of a promising youth but for the further fact that each plant was perfectly cross-fertile with every other plant. It did indeed reduce my interest in the inheritance of corolla size, for it precluded the study of an *F*₃ generation, but this was offset by the more fascinating problem of self-sterility.

² Ann. Roy. Bot. Gard. Peradeniya 4: 195-227. 1909.

³ The *Sandarae* hybrids were supposed to have been produced by the cross *N. forgetiana* × *N. alata grandiflora*.

It was impossible to study the F_3 generation because crosses between two F_2 individuals alike somatically would be without meaning, since nothing could be known of the gametic potentiality of each. Crosses between F_1 individuals, on the other hand, meant something, because they were alike gametically. Six F_1 crosses were made therefore, and from them were grown 828 plants.

TABLE I

FREQUENCY DISTRIBUTIONS FOR LENGTH OF COROLLA IN A CROSS BETWEEN *Nicotiana forgetiana* AND *N. alata grandiflora*

| Designation | Class centers in millimeters | | | | | | | | | | | | | | |
|-----------------------------------|------------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|----|
| | 20 | 25 | 30 | 35 | 40 | 45 | 50 | 55 | 60 | 65 | 70 | 75 | 80 | 85 | 90 |
| <i>N. forgetiana</i> , 314..... | 9 | 133 | 28 | | | | | | | | | | | | .. |
| <i>N. alata</i> gr. 321..... | | | | | | | | | | 1 | 19 | 50 | 56 | 32 | 9 |
| F_1 (314 \times 321)..... | | | 3 | 30 | 58 | 20 | | | | | | | | | .. |
| F_2 (314 \times 321) 1-6..... | .. | 5 | 27 | 79 | 136 | 125 | 132 | 102 | 105 | 64 | 30 | 15 | 6 | 2 | .. |

Table I shows the frequency distribution for length of corolla of *N. forgetiana* (314) inbred, *N. alata grandiflora* (321) inbred, the F_1 generation (314 \times 321), and the F_2 generation (314 \times 321) 1-6. The measurement was taken from the end of the pedicel to the center of the contraction commonly known as the corolla throat. The classes have a magnitude of 5 mm. and are centered at the even centimeters and half-centimeters. A glance at the distributions themselves is sufficient to show the small variability of the parent types and of the F_1 generation, and the great variability of the F_2 generation. The F_1 generation is strictly intermediate, as is the mean of the F_2 generation. *Among the individuals of the F_2 generation, however, are flowers identical with each parent.* This last fact is perhaps more clearly shown in the figures of pls. IX and X.

The statistical constants for each frequency distribution are shown in table II.

The spread of the corolla, measured to the tips of alternate lobes, behaved in the same way. Corolla breadth in *N. forgetiana* varied from 25-35 mm., with a sharp mode at 30 mm. The corolla spread of *N. alata grandiflora* was somewhat more variable in terms of the arithmetical standard, ranging from 55 mm. to 80 mm. The range of the F_1 individuals extended from 45 mm. to 55 mm.

In the F_2 generation plants were produced with a corolla breadth identical with each parent. In fact, there were four individuals as small as the smallest specimens of *N. forgetiana*, and there was one individual with flowers within 3 mm. of the size of those of the largest *N. alata grandiflora* growing in my cultures. The mean of this distribution was 48.57 ± 0.19 mm., the standard deviation 8.07 ± 0.13 mm., and the coefficient of variation 16.62 ± 0.28 per cent.

TABLE II

STATISTICAL CONSTANTS FOR FREQUENCY DISTRIBUTION OF TABLE I

| Designation | Mean | Standard deviation | Coefficient of variation |
|-----------------------------------|-----------------|--------------------|--------------------------|
| <i>N. forgetiana</i> , 314..... | 25.6 ± 0.12 | 2.27 ± 0.08 | 8.86 ± 0.33 |
| <i>N. alata</i> gr., 321..... | 78.8 ± 0.28 | 5.38 ± 0.20 | 6.82 ± 0.25 |
| F_1 (314 \times 321)..... | 44.3 ± 0.23 | 3.67 ± 0.17 | 8.28 ± 0.38 |
| F_2 (314 \times 321) 1-6..... | 49.9 ± 0.26 | 11.26 ± 0.19 | 22.57 ± 0.39 |

Examination of the F_2 generation of this cross indicated a correlation between the length of the corollas and the lengths of the filaments and the styles that for all practical purposes was perfect. By this statement I mean that the anthers were invariably just above the stigmas and the stigmas were invariably at the throat of the corolla. Of course absolute measurements would not show an integral coefficient of correlation, nevertheless one may assume, I think, that the fact is simply obscured by slight fluctuations. It seems as if the numbers were adequate from which to conclude either that the determiner or determiners of corolla length are also determiners of the length of the style and the filament or that these factor complexes are perfectly coupled in inheritance.

Corolla spread is also correlated with corolla length. It is by no means uncommon to find a sharp break in the correlation, as is witnessed by the individual with the very broad corolla and comparatively short tube pictured in pl. X, fig. 8; but one never finds inverse extremes in the same individual. Just what the correlation coefficient 0.610 ± 0.015 would prove to mean if individual analysis of later generations were made, is doubtful. We cannot go back of the gross statement that such a correlation exists

in the general population. Perfect coupling of certain factors together with independent combination of others may be possible; partial coupling arising from a peculiar gametic distribution may be equally possible.

TABLE III

CORRELATION BETWEEN LENGTH AND SPREAD OF COROLLA IN F_2 GENERATION OF
CROSS BETWEEN *N. forgetiana* AND *N. alata grandiflora*

Breadth of corolla in millimeters

| Length of corolla in millimeters | 25 | 30 | 35 | 40 | 45 | 50 | 55 | 60 | 65 | 70 | 75 | |
|----------------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 25 | 1 | ... | 4 | ... | ... | ... | ... | ... | ... | ... | ... | 5 |
| 30 | 2 | 5 | 4 | 10 | 3 | 3 | ... | ... | ... | ... | ... | 27 |
| 35 | 1 | 5 | 17 | 26 | 21 | 6 | 3 | ... | ... | ... | ... | 79 |
| 40 | ... | 6 | 12 | 38 | 41 | 31 | 7 | 1 | ... | ... | ... | 136 |
| 45 | ... | ... | 8 | 20 | 29 | 31 | 26 | 8 | 2 | 1 | ... | 125 |
| 50 | ... | ... | 3 | 22 | 30 | 44 | 25 | 7 | 1 | ... | ... | 132 |
| 55 | ... | ... | 1 | 2 | 22 | 27 | 37 | 9 | 4 | ... | ... | 102 |
| 60 | ... | ... | 1 | 3 | 11 | 32 | 29 | 19 | 9 | 1 | ... | 105 |
| 65 | ... | ... | ... | ... | 6 | 17 | 21 | 12 | 7 | 1 | ... | 64 |
| 70 | ... | ... | ... | 1 | 1 | 5 | 15 | 4 | 4 | ... | ... | 30 |
| 75 | ... | ... | ... | ... | ... | 7 | 3 | 4 | ... | 1 | ... | 15 |
| 80 | ... | ... | ... | ... | ... | 1 | 1 | 3 | ... | ... | 1 | 6 |
| 85 | ... | ... | ... | ... | ... | 1 | ... | ... | 1 | ... | ... | 2 |
| | 4 | 16 | 50 | 122 | 164 | 205 | 167 | 67 | 28 | 4 | 1 | 828 |

Coef. cor. 0.610 ± 0.015

These are the principal facts collected regarding this cross, if the small leaf differences and other minor variations are left out of consideration. How unimportant the latter are, can be seen by a reference to pl. VIII. There are several suggestions that may be made regarding the simple facts obtained, however, that may be helpful in further Mendelian interpretations of size complexes.

Elsewhere⁴ it has been shown that the behavior of such characters in crosses is adequately represented by the segregation and

⁴ Amer. Nat. 44:65-82. 1910.

recombination of cumulative unit factors that do not show the phenomenon of dominance. The frequency distribution of the F_2 generation in these cases is not $(\frac{3}{4} + \frac{1}{4})^n$, as it is where dominance is complete, but is $(\frac{1}{2} + \frac{1}{2})^{2n}$, because a factor in the heterozygous condition is to be regarded as producing one-half the effect that it produces when in the homozygous condition.

Regarding this expression as proper for the moment, let us examine the F_2 frequency distribution for length of corolla with the idea of assigning a definite number for n in the expression $(\frac{1}{2} + \frac{1}{2})^{2n}$.

If n is made equal to 3, then by the theory the F_2 distribution should have seven classes with the frequencies

1-6-15-20-15-6-1

per 64 individuals. For 828 individuals, the grandparental sizes should each be recovered $(828 \div 64) = 13.0 -$ nearly thirteen times. This was not the case in the actual distribution.

If n is made equal to 5, the F_2 distribution should have eleven classes with the frequencies

1-10-45-120-210-252-210-120-45-10-1

per 1024 individuals. With 828 individuals the grandparental classes should each be recovered only 0.8 times; in fact, a majority of populations of this size would not show the grandparental classes at all. This also is not the condition that was actually found.

There is left only the possibility of making n equal to 4. When this is done the F_2 distribution for 256 individuals—the smallest number in which a representative of each class may be found—and for 828 individuals is as follows:

1 - 8 - 28 - 56 - 70 - 56 - 28 - 8 - 1
3.2-25.9-90.6-181.1-226.4-181.1-90.6-25.9-3.2

This calculation points to the recovery of each grandparent about 3 times in the F_2 population under observation. Reference to table I shows that the figures actually obtained agree rather closely with this observation. But table I also shows another important fact. The arbitrary classes used had a range of 5 mm., which makes 13 classes necessary to express the F_2 generation.

This class size was adopted in accordance with the usual biometrical procedure, the variations in the small parent (314) being included in only 3 classes. But when this is done, the F_2 distribution is decidedly skew. The theoretical mode is along about the fourth or fifth class instead of the central class. What is the reason for the production of this type of curve? There must be a reason, and it seems to me that this reason must be biological and not a mathematical transnomination, as have been all the biometrical analyses of skew curves. The matter appears clear in the light of the following interpretation.

In ordinary statistical work, one produces a frequency distribution by throwing his tabular entries into arbitrary classes of equal size. By this procedure he has in all probability distorted their relationship. This fact is partially recognized by using the coefficient of variability instead of the standard deviation as a measure of variation. Unfortunately, it is usually said that the coefficient of variability is used instead of the standard deviation because it is an abstract measure and pounds can be compared with inches, etc. Standard deviations in the same concrete terms are usually thought comparable with each other. But is this true? Apply the rule to the data in tables I and II. The range of length of corolla of *N. forgetiana* (314) is 3 classes, the standard deviation is 2.27 ± 0.08 mm., and the coefficient of variability is 8.86 ± 0.33 per cent. The range of *N. alata grandiflora* (321) is 6 classes, its standard deviation is 5.38 ± 0.20 mm., and its coefficient of variability is 6.82 ± 0.25 per cent. Comparing standard deviations, *N. alata grandiflora* is twice as variable as *N. forgetiana*. Comparing coefficients of variability, which being functions of the mean give weight to the size of the mean, the large-flowered type (321) is less variable than the small-flowered type (314).

Let us now look at the matter from an ordinary common-sense biological standpoint. These pure line populations may be considered as composed of near-homozygous individuals. The range of variability shown is therefore almost wholly due to environment. In general, *N. alata grandiflora* has a corolla more than twice as long as *N. forgetiana*. Is it not reasonable to suppose that the unit change effected by environment and expressed as a

fluctuation is proportional to the size of the individual? Is it not true that favorable circumstances which force the corollas of *N. forgetiana* to become 5 mm. longer than usual will produce a 10 mm. change in *N. alata grandiflora*?

If this is the correct way of looking at these two cases, then it is assuredly an error to plot the F_2 distribution—which includes both grandparental sizes—in classes of equal size. Assuming that our hypothetical size factors affect the individual as growth forces, it seems probable that they are not only cumulative but accelerative. Roughly one might imagine the effect on the individual to be something like a constant percentage. I do not believe these cases of size inheritance can be analyzed into their component factors and these factors given their proper weight (using the word factor in the general sense of elements or causes that produce a result) sufficiently well to give a precise value to the character determiners themselves. On the other hand, it is interesting to see just what is necessary in the way of class range to bring our F_2 corolla distribution to the normal distribution for four factors ($n=4$). Fortunately the corolla sizes were taken by millimeters, so this can be done. First I have smoothed the figures according to the regular method. The distribution in one-millimeter classes is then as follows (table IV, p. 186).

Suppose now we begin at 24 mm. and take for this class a range of 4 mm. Then let us increase our class range 1 mm. each time. This gives a simple arithmetical progression with an advancing difference of the second order, that is, the differences between the class ranges are constant. Compare the frequency distribution thus obtained with the expansion of $(\frac{1}{2} + \frac{1}{2})^{2n}$ where n is equal to 4. This is done in table V, with an agreement among the figures that is very remarkable. If I were a biometrist, I probably could show that this agreement could not be due to chance—since by chance it could only occur once in some hundreds of thousands of times—and must therefore have some great significance. I should prefer to believe that I happened by chance upon a series of class ranges that fitted the normal frequency theory. But it must be emphasized that it was a *constant* increase in class range that produced the normal curve from the distorted skew curve.

Perhaps no two actual frequency distributions would be alike in thus yielding to a simple arithmetical correction. Such a correction is probably fallacious in its simplicity. It serves our purpose,

TABLE IV

MEASUREMENTS OF LENGTH OF COROLLA IN F_2 POPULATION OF CROSS BETWEEN
Nicotiana forgetiana AND *N. alata grandiflora*

| Size mm. | freq. | Size mm. | freq. | Size mm. | freq. |
|----------|-------|----------|-------|----------|-------|
| 24 | 0 | 45 | 25 | 66 | 12 |
| 25 | 2 | 46 | 28 | 67 | 10 |
| 26 | 2 | 47 | 29 | 68 | 7 |
| 27 | 2 | 48 | 28 | 69 | 7 |
| 28 | 1 | 49 | 28 | 70 | 6 |
| 29 | 3 | 50 | 26 | 71 | 6 |
| 30 | 5 | 51 | 28 | 72 | 5 |
| 31 | 8 | 52 | 23 | 73 | 6 |
| 32 | 10 | 53 | 20 | 74 | 4 |
| 33 | 11 | 54 | 20 | 75 | 3 |
| 34 | 15 | 55 | 19 | 76 | 2 |
| 35 | 13 | 56 | 22 | 77 | 2 |
| 36 | 18 | 57 | 22 | 78 | 0 |
| 37 | 18 | 58 | 22 | 79 | 1 |
| 38 | 19 | 59 | 26 | 80 | 2 |
| 39 | 26 | 60 | 21 | 81 | 2 |
| 40 | 28 | 61 | 22 | 82 | 1 |
| 41 | 33 | 62 | 15 | 83 | 0 |
| 42 | 24 | 63 | 15 | 84 | 1 |
| 43 | 23 | 64 | 14 | 85 | 0 |
| 44 | 24 | 65 | 12 | 86 | 1 |

TABLE V

COMPARISON BETWEEN THE THEORETICAL FREQUENCY DISTRIBUTION FOR FOUR FACTORS
AND THE ACTUAL FREQUENCY DISTRIBUTION RESULTING WHEN CLASSES
WITH A CERTAIN CONSTANTLY INCREASING RANGE ARE USED

| Class limits | 24-27 | 28-32 | 33-38 | 39-45 | 46-53 | 54-62 | 63-72 | 73-83 | 84-95 |
|--|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Class range..... | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| Frequency..... | 6 | 27 | 94 | 183 | 210 | 189 | 94 | 23 | 2 |
| Calculated frequency for 828 individuals for $(\frac{1}{2} + \frac{1}{2})^8$ | 3.2 | 25.9 | 90.6 | 181.1 | 264.4 | 181.1 | 90.6 | 25.9 | 3.2 |

however, if it calls attention to the manifest error of expressing a wide range of biological variation by a frequency polygon of equal size classes.

Summary

Concluding, the following points may be again emphasized:

1. The inheritance of size complexes is so intricate that it is necessary to simplify an experiment upon them in every possible manner. The material used in this investigation, *Nicotiana forgetiana* Hort. Sand. and *N. alata grandiflora* Comes, lacks three of the complicating features that usually ensnarl such work. They are almost always naturally self-fertilized, and through numerous generations of self-fertilization have become automatically as homozygous in their characters as may be expected in plants that reproduce sexually. Their fecundity is so great that practically any quantity of F_2 individuals can be produced from a single F_1 plant. A plant character was investigated upon which the effect of environment is so small as to be negligible, namely corolla size.

2. These self-fertile species, which are perfectly fertile *inter se*, gave self-sterile progeny. This fact did not affect the production of an F_2 generation, as the F_1 plants from homozygous parents are alike in gametic constitution, and these were perfectly fertile *inter se*.

3. *N. forgetiana* with a mean corolla length of 25.6 mm. crossed with *N. alata grandiflora* with a mean corolla length of 78.8 mm. resulted in an intermediate F_1 generation with a mean variability of 44.3 mm.

4. The variability of the F_1 generation was very small, being about the same as that of the remarkably constant parental species. The F_2 generation, on the contrary, was very variable and both grandparental types were reproduced.

5. It is shown that the F_2 generation is what would be expected if the difference in corolla length shown by these two species were represented by the segregation and recombination of four cumulative but independent pairs of unit factors, dominance being absent.

6. The coincidence of theory and result is as great in this case as it is in qualitative characters of like complexity. If the Mendelian notation is useful to describe complex qualitative inheritance, it is similarly useful in describing the inheritance of quantitative characters.

7. Length of style and of filament are perfectly correlated with corolla length.

8. Breadth of corolla shows an average correlation with length of corolla equal to 61 per cent.

9. The frequency distribution of corolla length for the F_2 generation is positively skew. It is pointed out that the range of fluctuations of corolla length in the two pure species is twice as great in the one of larger size than in the other. Classes of equal size in frequency distributions of great variability appear to be arbitrary and improper, if size factors are assumed to be dynamic factors with fluctuations roughly expressed by the term growth force. To show this accelerative action, the class ranges must gradually increase as the size (that is, the number of factors) increases. It is shown that the distribution under discussion will be changed from skew to normal if a simple arithmetical increase in the size of the classes is made.

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EXPLANATION OF PLATES

PLATE VI

At the left, a young flowering plant of *Nicotiana alata* Link and Otto, var. *grandiflora* Comes; at the right, a young flowering plant of *N. forgetiana* Hort. Sand.

PLATE VII

A mature plant of the first hybrid generation of a cross between *N. forgetiana* and *N. alata grandiflora*.

PLATE VIII

Figs. 1, 2, and 3, upper, median, and lower leaves of a mature plant of *N. alata grandiflora*; figs. 4, 5, and 6, upper, median, and lower leaves of the first generation of a cross between *N. forgetiana* and *N. alata grandiflora*; figs. 7, 8, and 9, upper, median, and lower leaves of a mature plant of *N. forgetiana*.

PLATE IX

At the left, a flower of *N. alata grandiflora*; at the right, a flower of *N. forgetiana*; between them are extreme F_2 segregates in length and spread of corolla; taken on the same plate, three-fourths natural size.

PLATE X

Fig. 1, *N. alata grandiflora*; fig. 2, *N. forgetiana*; fig. 3, cross between *N. forgetiana* and *N. alata grandiflora*, F_1 generation; the remaining figures are F_2 segregates; all figures are three-fourths natural size.





EAST on NICOTIANA



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